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TWO CYNODONTS FROM THE NTAWERE FORMATION IN THE LUANGWA VALLEY OF NORTHERN RHODESIA

By A. S. Brink

ABSTRACT

Two Cynodonts, *Diademodon rhodesiensis* sp. nov. and *Luangwa drysdalli* gen. et sp. nov., are described in this paper. In structure both forms indicate that the Ntawere Formation in the upper Luangwa valley of Northern Rhodesia from which they were collected can be regarded as very late *Cynognathus*-zone, perhaps mostly Molteno, compared with the South African succession, or of the same age as the Manda Beds of the more nearby Ruhuhu valley of Tanganyika. The *Diademodon* specimen is very similar to its South African relatives, but in some details it is more advanced. The new genus *Luangwa* has its closest ally in the Ruhuhu form *Scalenodon*.

INTRODUCTION

With the kind co-operation of the Geological Survey of Northern Rhodesia, the Bernard Price Institute undertook two expeditions into the remote and isolated northern part of the Luangwa valley to investigate more closely the areas from which Dixey collected some Karroo Therapsida in 1928 and 1935 (Dixey, 1937), previously noticed by Wallace in 1907, and subsequently described by Boonstra in 1938. The first expedition was undertaken during July, August and September 1960 and the second during the same months of 1961. On both occasions Dr. A. R. Drysdall of the Geological Survey of Northern Rhodesia accompanied our Field Officer, Mr. J. W. Kitching, to attend to the detailed geological interpretation of the area, while Mr. Kitching could devote all his attention to the locating of fossiliferous horizons and the actual recovery of fossil specimens.

Drysdall and Kitching have published in the Transactions of the Geological Society of South Africa a report based on the first expedition, while a more comprehensive analysis of the results of both expeditions is to be published by the Geological Survey of Northern Rhodesia. An article in which Kitching sketches more specifically his own valuable impressions of the general palaeontological background and field conditions vital to the present and all subsequent papers devoted to the description of the material will be published by the South African Journal of Science as a contribution to a symposium.

Under the highly appreciated and kind auspices of the Rhodes-Livingstone Museum of Livingstone, Northern Rhodesia, I was enabled to visit the expedition in the field in 1960, in the company of Mr. J. Chaplin, archaeologist of the above Museum. I could thus gain first hand information on the nature of the Karroo beds in this area and the manner in which the therapsid specimens occur in situ.

The second expedition has produced a great deal of information complementary to that already recorded, as well as some findings which dictated corrections of

certain already formulated opinions. Most important of these was the discovery that the Ntawere Formation, originally interpreted by Dixey (1937) as "Dinosaur Beds" of Cretaceous age, is not of upper Stormberg age as Drysdall and Kitching concluded after their first expedition, but is of late *Cynognathus*-zone age, extending well into the lower Stormberg.

On the occasion of the first expedition Kitching discovered Dixey's so-called "Dinosaur" rolled bones deposited in the Ntawere Formation and identified them as anomodont limb bones derived from the denudation and redeposition of the earlier Karroo strata of *Cistecephalus* and *Endothiodon*-zone age. This, Drysdall and Kitching interpreted, had occurred at approximately the Red Beds level in the upper Karroo, to correlate satisfactorily with the underlying Escarpment Grits which they took as upper Beaufort, and the overlying Red Marls and Upper Grits.

With the second expedition Kitching discovered in the Ntawere Formation some specimens typical of the *Cynognathus* zone of the South African Karroo, which were not secondarily redeposited like the anomodont bones; they occur as primary fossils embedded at the time of deposition of the Ntawere Formation. All these fossils differ from the earlier *Cistecephalus* and *Endothiodon*-zone specimens from the same general area in the nature of the matrix and in that they all appear to have suffered some weathering and deterioration before they became embedded. The surfaces of the bones are corroded, cracked and otherwise damaged, usually more particularly on one side, but internal structures are better preserved and the softer matrix permits more successful development than in specimens from the lower horizons, which are usually associated with the most difficult, incredibly hard ironstone matrix.

The present interpretation places the Ntawere Formation at the level of the uppermost part of the *Cynognathus*-zone, with substantial overlap into the Molteno beds. The unfossiliferous Escarpment Grits could then correlate with the South African *Lystrosaurus* zone, while the Red Marls and Upper Grits conform with the Red Beds and Cave Sandstones of the Stormberg.

On account of the remoteness and inaccessibility of the area, and the rough and wild terrain across which the actual field work had to be done, the expedition was on both occasions limited in scope and, however unfortunate, some of the more badly preserved and incomplete specimens had to be left behind, because they would not have survived the hazardous cross-country transport. Some large specimens had to be carried on foot for six and eight miles across rocky ranges and jungle terrain teeming with herds of buffalo and elephant. Those that could be recovered number 279 good individuals from the first expedition and 217 from the second; a total of 496 fair to good skulls, some with associated skeletons or portions of skeletons.

The specimens recovered from the Ntawere Formation on the second expedition are three large Rhinesuchid-like amphibian skulls, a *Kannemeyeria*-like anomodont, another large anomodont somewhat *Stahleckeria*-like in superficial

appearance, a small badly preserved *Trirachodon*-like snout, a *Diademodon* and another new *Scalenodon*-like gomphodont. The latter two are described in this paper.

Diademodon rhodesiensis sp. nov.

(Figures 12, 13, 14)

In contrast with the other above-mentioned forms which merely bear a superficial resemblance to certain known forms as indicated, the present specimen is very typically a *Diademodon* and it is very difficult to find a particular feature about the skull on the strength of which it can emphatically be differentiated from a known species like *D. polyphagus* (with which it agrees more closely than with any of the other known species). The great distance between the locality of this specimen and those of its South African relatives (2,000 miles) can in itself warrant its recognition as a separate species. There are, however, some additional features which, although difficult to contrast with some inadequately known species, point not only to specific distinction but also to the fact that this species is somewhat more advanced than the South African forms. Its locality could also be within the Molteno level.

There are some peculiarities which should not readily be interpreted as diagnostic of the new species; it would appear rather that existing information regarding the South African species is somewhat incomplete or even inaccurate. These peculiarities are found mostly in the lower jaw.

The dentary has a powerful articular process clearly distinguishable from the coronoid process above and the angular process below. The other lower jaw bones seem to be more reduced than has been the interpretation so far, based on the South African forms. The articular-prearticular rod is still dominant, associated with a reduced angular, but the surangular seems to be even more reduced, while the coronoid is practically vestigial. Both splenials have fallen away before fossilization. The surangular fits into a well defined short groove posteriorly in the dentary. The area of insertion of the prearticular-angular rod at a slightly lower level is not well demarcated. With these bones removed, as they are on the right side in the specimen, the dentary bears a rather striking resemblance, in general build, to that of the so-called "Rhaetic mammals".

To accommodate the powerful roots of the elaborate postcanine teeth of *Diademodon* (and *Cynognathus*) there is a significant thickening of the dentary in the shape of a fold medially, growing backwards as the number of teeth increased with age. This fold abuts against the flatter and thinner posterior part of the dentary in a manner suggesting a "suture". This "suture" has apparently on occasions been interpreted as the posterior, dorsal, or postero-ventral margin of the coronoid, the other margins having been obscured by matrix or bad preser-

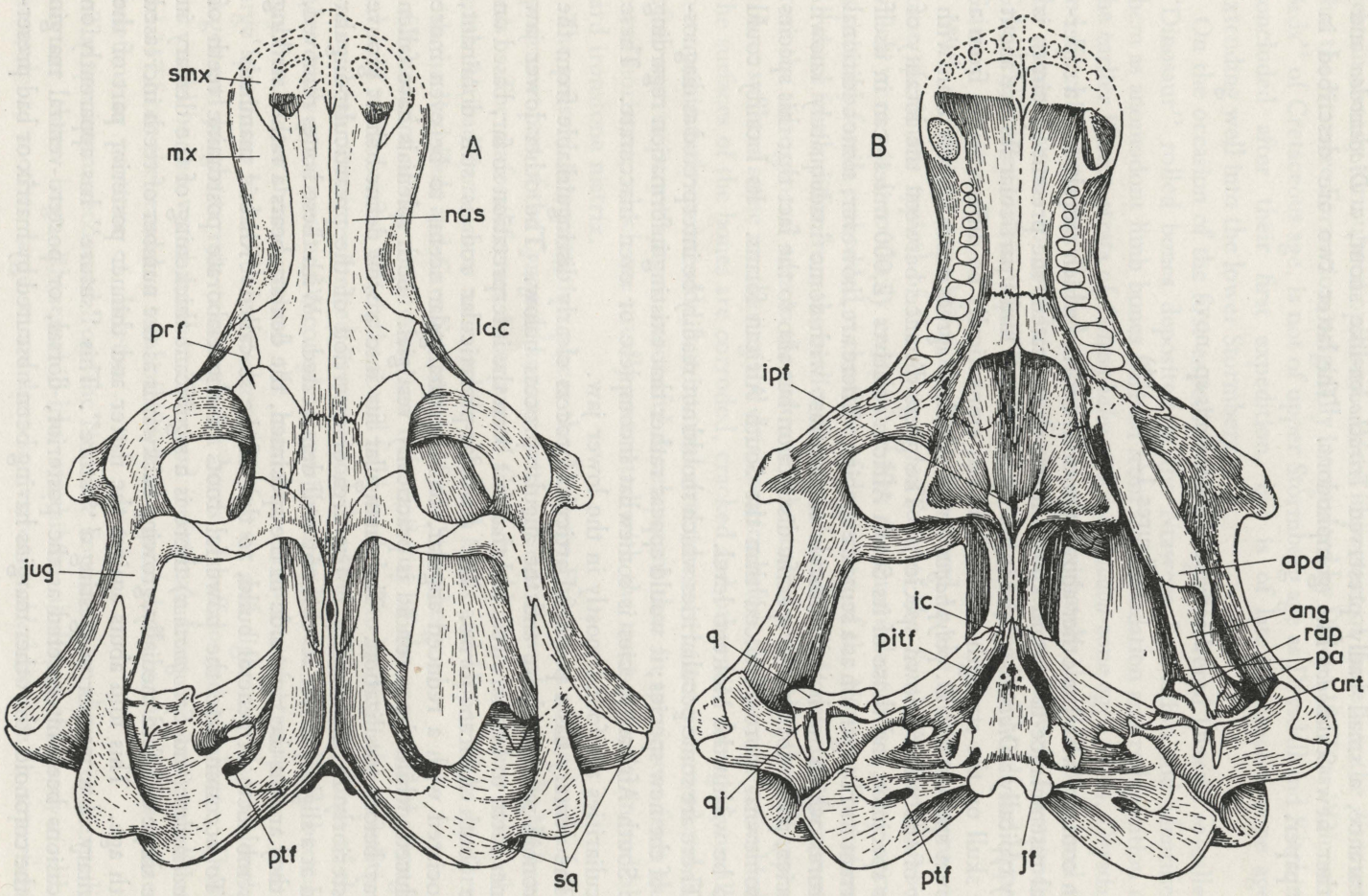


Fig. 12—A, Dorsal and B, Ventral view of the skull of *Diademodon rhodesiensis* sp. nov., ½ natural size: For abbreviations see figure 13.

vation. In the present specimen the coronoid is a distinctly separate bone lying farther back, with a rather conspicuous process overlapping the surangular.

It had been the impression, perhaps judging more from the condition in lower cynodonts, that should the splenial be removed, the Meckelian canal would be exposed along its whole length. In the present specimen both splenials are removed and on both sides the canal is still elaborately covered by a substantial fold of the dentary arising along the dorsal border and extending downward (below the splenial) to cover the lower margin of the canal quite extensively. Where this fold abuts against the lower margin of the dentary, a very conspicuous "suture" is formed which may also have been interpreted in other specimens as the ventral margin of the splenial where, as in the present specimen, the splenial had actually fallen away. It would appear that the interpretation put forth by Broili and Schröder (1935) had become confused by this arrangement. Their coronoid is also most unlike the coronoid of the present specimen and undoubtedly represents the alveolar fold of the dentary. This most ambiguous arrangement had induced me to arrive at similar conclusions while studying less well preserved material (Brink, 1955).

The actual structure of the dentary itself is clearly displayed and it is accurately portrayed in the accompanying figure 14. There is a powerful symphysis, the height of the "chin" being less prominent than in *Cynognathus*. The Meckelian canal opens in front inside the symphysial contact surface but, besides being continuous with the canal of the other dentary, a mesial canal extends directly back between the two dentaries to open in the angle between the two mandibles, immediately above their ventral margins. The splenials apparently do not cover this opening.

The fold of the dentary extending downward and elaborately covering the Meckelian canal forms a prominent bulge anteriorly, above and mesially to the anterior end of the canal, communicating with a similar bulge of the other dentary. In more primitive forms the splenials are normally expanded similarly anteriorly where they contribute to the symphysis. This bulge has been interpreted in *Diademodon* as belonging to the splenial, but in the present specimen at least the splenial had no doubt been considerably reduced in this area, more like the splenial in *Scalenodon* (Crompton, 1955) or that of the specimen described below as *Luangwa*.

The ventral margin of the mandible is straight, heavily thickened and well rounded. This almost rod-like margin grows thicker and more powerful backward and terminates very abruptly as the angular process some distance below and shortly in front of the articular region.

The margin of the dentary continues upward and backward from this angular process to the articular region as a thin sharp edge, curving concavely inwards alongside the angular bone. At the articular region it curves sharply outward and around the surangular bone, immediately dorsally to which it turns straight inwards and, still farther back, to reach across a seat or bulge in the dorsal surface

of the posterior end of this bone. This bulge lies farther back than in the South African forms in which this condition is known.

On the inner face of this part of the dentary a prominent groove is thus formed, accommodating the surangular rod. The ventral border of this groove is slightly prominent, but the dorsal margin is heavily thickened and forms a powerful structure to enhance the mechanical strength of the articulation with a view to the masticatory commitments to which the jaw is subjected, as evidenced by the dentition, the strong coronoid processes, the tall parietal crest and powerful zygomatic arches.

The quadrates in *Diademodon*, and apparently in all cynodonts, were streptostylic. The wear on *Diademodon* post-canine teeth shows that the lower jaw was capable of some reasonable antero-posterior movement, and this occurred with the collaboration of the quadrates. The pterygoid processes and the pits in the anterior palate receiving the lower jaw canines certainly made lateral movement of the lower jaw, as an alternative movement to account for the wear on the postcanine teeth, completely impossible. Muscles extending from the prominent angular processes of the dentaries to the jugal processes caused the lower jaw to move forwards on contraction. Antagonistic muscles for drawing the jaw backwards (part of the digastric) apparently extended from both the outer and inner surfaces of the dentaries, above the angular processes, to the prominent angles formed at the extreme posterior ends of the jugals, laterally to the quadrates. These muscles were inserted in depressed areas below the articular-angular rod which are clearly distinguishable from the larger areas of insertion of the masseter and temporal muscles.

On drawing the lower jaw back, the dentary would, theoretically, not have had the opportunity of actually making contact with the squamosal laterally to the quadrate, because the articular expands laterally and it presents a distinct shoulder against which the posterior margin of the dentary is destined to abut; in the natural condition it would appear, however, that the dentary did not reach quite this far back. But the more powerful portion of the dentary forming the actual articular process immediately dorsally to the articular could theoretically have come in contact with the squamosal above the quadrate, with the lower jaw drawn back as far as possible, as though with the object of limiting the extent to which the lower jaw can move backward, where otherwise the articular might dislodge the quadrate from its rather delicate articulation with the squamosal. In practice, however, this prolongation of the dentary had stopped short of the squamosal, while the laterally expanded articular had areas either side of the quadrate against which it could abut.

The structure nevertheless portrays a condition not too remotely ancestral to the more advanced double articulation of *Diarthrognathus* (Crompton, 1958). With some reduction of the lateral expansion of the articular which would appear to intervene between the dentary and the squamosal laterally to the quadrate,

and the stronger development of the dentary at this point rather than at its present more dorsal level, the double articulation condition can be achieved.

Another substantial difference between the lower jaw of the new specimen and that of the South African forms is to be found in the coronoid process. In the present specimen the posterior margin of the coronoid process is more deeply concave and the dorsal extremity curves more powerfully backward to a level well beyond that of the articular process.

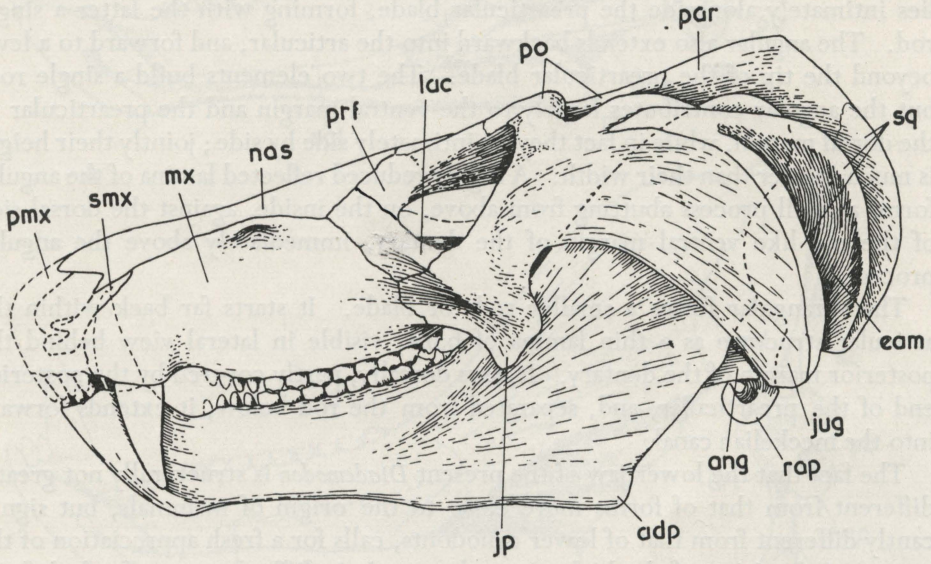


Fig. 13—Lateral view of the skull of *Diademodon rhodesiensis* sp. nov., ½ natural size. Abbreviations: **adp,** angular process of the dentary; **ang,** angular; **ardp,** articular process of the dentary; **art,** articular; **cor,** coronoid; **cp,** coronoid process; **eam,** external auditory meatus channel; **ic,** internal carotid foramen; **ipf,** interpterygoid fossa; **jug.** jugal; **jf,** jugular foramen; **jp,** jugal process; **lac,** lachrymal; **mc,** meckelian canal; **mx,** maxillary; **nas,** nasal; **pa,** prearticular; **par,** parietal; **pmx,** premaxillary; **po,** postorbital; **prf,** prefrontal; **ptf,** postemporal fossa; **q,** quadrate; **qj,** quadratojugal; **rap,** reatroarticular process; **rl,** reflected lamina of the angular; **sa,** surangular; **smx,** septomaxillary; **spl,** splenial; **sq,** squamosal.

The prearticular and angular bones form a rod of greater vertical than transverse thickness. Anteriorly these two bones penetrate side by side underneath the fold covering the meckelian canal, and ventrally to the latter. Here it may also have been covered to some extent by the posterior end of the splenial. The anterior end of the surangular rod penetrated dorsally into the canal itself and was additionally covered by a process of the coronoid. In the specimen the whole structure on the left side is complete, but it is neatly dislodged from the dentary which had been forced a short distance backward and outward. It is nevertheless still in perfect articulation with the quadrate and in a true and natural relationship to

the rest of the skull, and its actual association with the dentary can be ascertained quite accurately. The articular forms a structure quite considerably larger than the quadrate. Ventrally it forms a peculiar horn-like retroarticular process which curves sharply forward and inward. This process is larger in *Diademodon* than in *Cynognathus* and it appears to be insubstantially ossified.

The whole of the blade portion of the articular-prearticular unit consists of the prearticular bone and it penetrates well back into the articular, which is confined to the portion forming the structure articulating with the quadrate. The angular lies intimately alongside the prearticular blade, forming with the latter a single rod. The angular also extends backward into the articular, and forward to a level beyond the tip of the prearticular blade. The two elements build a single rod, but the angular contributes largely to the ventral margin and the prearticular to the dorsal margin, while in fact they lie intimately side by side; jointly their height is much greater than their width. A highly reduced reflected lamina of the angular forms a small process abutting from above, on the inside, against the dorsal side of the rod-like ventral margin of the dentary, immediately above the angular process.

The surangular forms a smaller rod, or blade. It starts far back within the articular structure as a thin lamina of bone, visible in lateral view behind the posterior margin of the dentary. It rises dorsally, partly covered by the posterior end of the prearticular, and, separated from the rod below, it extends forward into the meckelian canal.

The fact that the lower jaw of the present *Diademodon* is structurally not greatly different from that of forms more close to the origin of mammals, but signif-cantly different from that of lower cynodonts, calls for a fresh appreciation of the taxonomic position of the higher cynodonts. It is difficult to put forth definite suggestions at this stage while many cynodont lower jaws are still inadequately known. However, it does seem that within the Cynodontia as diagnosed at present there are two strikingly different types of lower jaws. The lower procynosuchid-thrinaxodontid cynodonts and other more primitive silphedestids are all characterised in contrast by a dentary lacking both the angular and the articular processes and by the fact that the dentary does not extend nearly as far into the articular region. The other lower jaw bones also form a rather different and characteristic picture. The surangular is invariably powerfully arched and has a distinct reinforcement role. The angular is elaborately exposed in lateral view and the reflected lamina is a conspicuous freely projecting fan with quite obviously a substantially different function from that of the higher cynodonts. It also appears from the material of *Procynosuchus*, *Leavachia* and *Thrinaxodon* at hand that the arrangement as far as the splenial and coronoid are concerned is more comparable with that of the serially sectioned *Scalopocynodon* (Brink 1960a) than with the higher cynodonts.

These conspicuous differences in the lower jaws alone, between the higher and lower cynodonts, especially with respect to features so crucial in terms of the

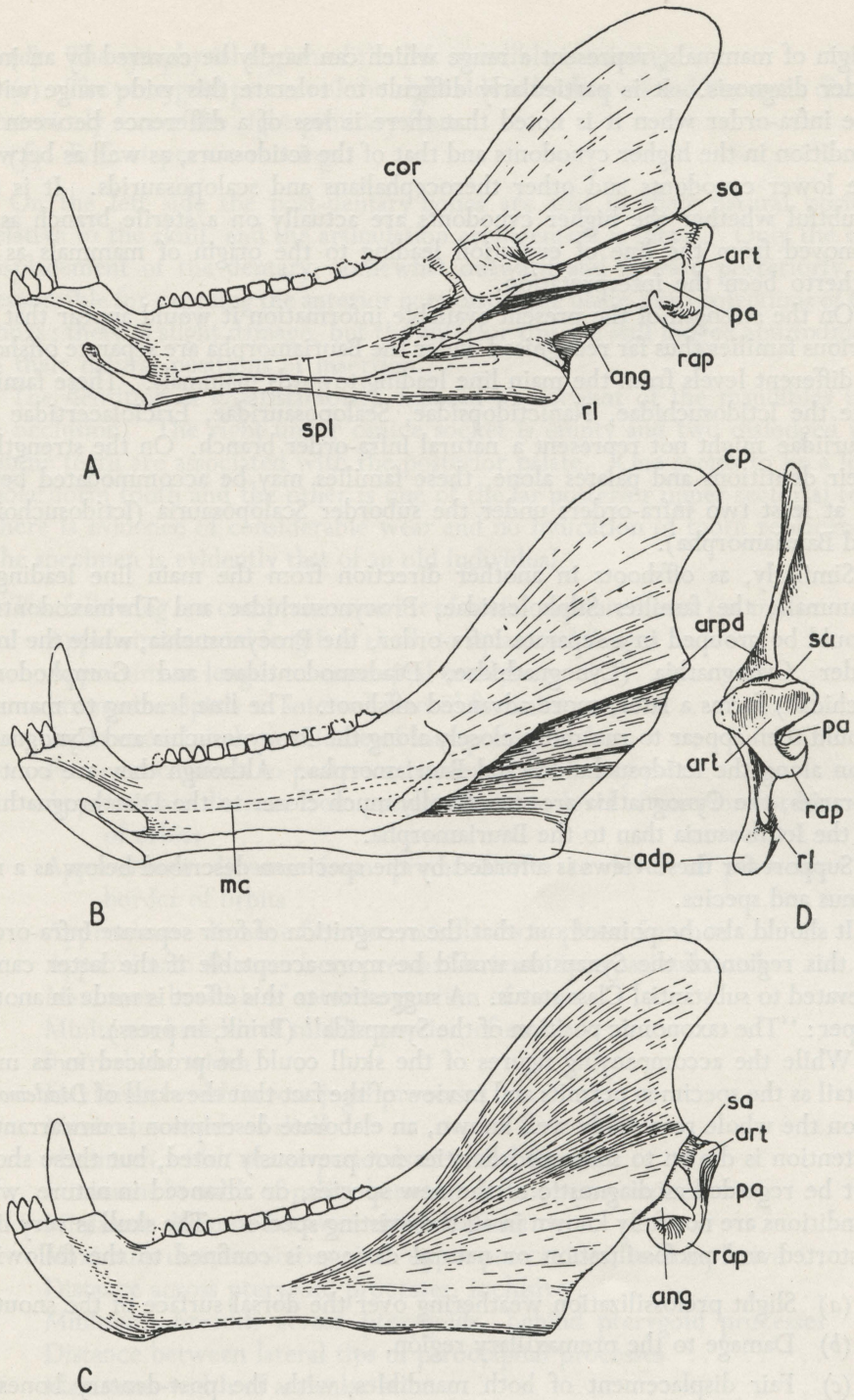


Fig. 14—The lower jaw of *Diademodon rhodesiensis* sp. nov., ½ natural size. A, Internal view; B, Internal view with post-dentary bones removed; C, External view; D, Posterior view. For abbreviations see figure 13.

origin of mammals, represent a range which can hardly be covered by an infra-order diagnosis. It is particularly difficult to tolerate this wide range within one infra-order when it is noted that there is less of a difference between the condition in the higher cynodonts and that of the ictidosaurs, as well as between the lower cynodonts and other therocephalians and scaloposaurids. It is also doubtful whether the higher cynodonts are actually on a sterile branch as far removed from the line of evolution leading to the origin of mammals as has hitherto been the interpretation.

On the strength of the present available information it would appear that the various families thus far recognised under the Bauriamorpha are separate offshoots at different levels from the main line leading towards mammals. These families like the Ictidosuchidae, Nanictidopsidae, Scaloposauridae, Ericiolacertidae and Bauriidae might not represent a natural Infra-order branch. On the strength of their dentitions and palates alone, these families may be accommodated better in at least two infra-orders under the suborder Scaloposauria (Ictidosuchoidae and Bauriamorpha).

Similarly, as offshoots in another direction from the main line leading to mammals, the families Silpholestidae, Procynosuchidae and Thrinaxodontidae should be grouped in a separate Infra-order, the Procynosuchia, while the Infra-order Cynognathia (Cynognathidae, Diademodontidae and Gomphodonto-suchidae) forms a later, more advanced offshoot. The line leading to mammals would then appear to run more closely along the Procynosuchia and Cynognathia than along the Ictidosuchoidea and Bauriamorpha. Although they are contemporaries, the Cynognathia are structurally much closer to the Diarthrognathidae of the Ictidosauria than to the Bauriamorpha.

Support for these views is afforded by the specimen described below as a new genus and species.

It should also be pointed out that the recognition of four separate Infra-orders in this region of the Synapsida would be more acceptable if the latter can be elevated to substantial Class status. A suggestion to this effect is made in another paper: "The taxonomic position of the Synapsida" (Brink, in press).

While the accompanying figures of the skull could be produced in as much detail as the specimen permits and in view of the fact that the skull of *Diademodon* is on the whole reasonably well known, an elaborate description is unwarranted. Attention is drawn to some peculiarities not previously noted, but these should not be regarded as diagnostic of the new species, or advanced in nature, while conditions are not fully known in all the existing species. The skull is very little distorted and prefossilization or natural damage is confined to the following:

(*a*) Slight prefossilization weathering over the dorsal surface of the snout.

(*b*) Damage to the premaxillary region.

(*c*) Fair displacement of both mandibles, with the post-dentary bones on the left side slightly, and on the right side completely, dislodged.

(*d*) The symphysial region of the left mandible is missing.

(*e*) The pterygoid process of the right side is broken off and lies some distance posteriorly across the right pituitary fossa.

(*f*) Both stapes are missing.

On the left side the post-dentary bones are still in their natural position, relative to the skull, and the articulation arrangement is intact. Only the slight displacement of the dentary, somewhat outward and upward posteriorly, was responsible for exposing the anterior portions of the blade-like projections of these bones; there is slight damage, but the anterior tips are still lodged approximately in their natural positions of insertion.

The dentition is unsatisfactorily exposed on account of the mandibles being in occlusion. The right upper canine socket is empty and two dislodged post-canine teeth are associated with the posterior palate. One seems to be a lower molariform tooth and the other is one of the far posterior upper sectorial teeth. There is evidence of considerable wear and no indication of tooth replacement. The specimen is evidently that of an old individual.

The following is a comprehensive list of useful measurements (in mm):

Approximate total length of skull, to squamosal flanges	236
Approximate length to exoccipital condyles	215
From exoccipitals to internal carotid foramina	45
From exoccipitals to middle of interpterygoid fossa	80
From exoccipitals to posterior border of secondary palate	121
Approximate distance from premaxillaries to level of anterior border of orbits	102
Approximate distance from premaxillaries to level of posterior border of orbits	140
Approximate distance from premaxillaries to pineal foramen	165
Approximate distance from premaxillaries to interparietal notch	207
Maximum breadth of anterior portion of snout	53
Minimum breadth of middle portion of snout	42
Interorbital width	40
Maximum width across jugal processes	140
Maximum width of skull	173
Minimum width across parietals at pineal foramen	25
Minimum breadth of palate between anterior postcanines	21
Minimum distance between upper canines	33
Maximum distance across ninth upper postcanines, both inclusive	75
Distance across pterygoid processes, inclusive	55
Minimum breadth across pterygoids, behind pterygoid processes	14
Distance between lateral tips of paroccipital processes	86
Maximum width of articular bone	30
Maximum width of quadrate condyle	23

From anterior tip of dentary to articular process, direct	188
From anterior tip of dentary to angular process, direct	152
From anterior tip of dentary to coronoid process, direct	205
Maximum vertical height of dentary	106
Height of dentary at anterior postcanines	25
Length of row of nine molariform postcanines, upper	52

I have previously indicated (Brink, 1955) that the series of nine molariform postcanine teeth is inclined to measure a rather constant length for a particular species, irrespective of substantial differences in the size of the skull in terms of age, and that these lengths differ quite conspicuously among the species. In the present specimen the nine postcanine teeth measure 52 mm., which agrees best with *D. polyphagus*.

The following are some interesting observations on the present skull:

(1) There is a very narrow slit-like interpterygoid fossa extending across a ridge between two very prominent small bosses in the area between the pterygoid processes. The presence of this fossa has not been noted before in *Diademodon*. It is quite decidedly absent in a new specimen in the collection of this Institute, which will be described in due course. This region is of course not properly known or well enough investigated in the majority of the South African species, so that it is difficult to decide whether this feature is characteristic of the new species only. The presence of this fossa, at least in the present species, shows that *Diademodon* is perhaps not as far diverted on a sterile lateral branch to the line leading towards mammals as has hitherto been the interpretation. However, the position of this fossa is different from that of *Leavachia*, *Scaloposaurus* and *Bauria*, as well as that of *Diarthrognathus*. In these forms the interpterygoid fossa lies more posteriorly. The arrangement in the present specimen is, on the other hand, similar to that of the primitive *Scalopocynodon*.

(2) The internal carotid foramina are exceptionally small. They are very narrow slits in the parasphenoid-alisphenoid suture immediately behind the pterygoid suture, some 6 mm. above the ventral edge of the parasphenoid keel.

(3) The foramen for the seventh nerve is larger, and it lies closer to the fenestra ovalis in the posterior wall of the pituitary fossa than has been apparent in the material previously investigated. This observation is important, because the facial nerve is more prominent in mammals than in reptiles. It innervates the fleshy structures of the snout which, in mammals, are more characteristically mobile and expressionable, and also more sensory. This is interesting too in view of the large nervous foramina penetrating the maxillaries above the postcanine teeth and other evidence pointing to the more mammal-like glandular and sensory nature of the snout and nostril regions (Brink, 1955, 1956, 1960b). In two new specimens of *Diademodon*,

described in another paper (p. 27 of this issue) new evidence has also come to light on muscular arrangement in the nostril area.

(4) The ventral surface of the paroccipital process is very deeply excavated to form a high domed roof to the middle ear. The pterygo-paroccipital foramen penetrates dorsally through the middle of this roof.

(5) The external auditory meatus groove continues inward around an anterior bulge, the quadrate processes of the paroccipital, to the position of the tympanum, which appears to have been situated a great deal farther internally than previously investigated materials have suggested.

(6) The quadrate, and especially its articular condyle, is a much more delicate structure than hitherto interpreted. It is very elementary compared with the complex structure formed by the articular bone, which articulates with it. The condyle itself is a delicate elongated dumbell-shaped structure, the two condyles thus formed on either side having long axes extending parallel ventrolaterally at angles of 45° to the vertical plane of the skull, and within the transverse plane. The lateral condyle is supported by a wedge cutting straight antero-posteriorly across the tranverse squamosal wall, but the medial condyle has, in addition to a similar but shorter and stouter wedge, also a flange continuous with it, which swings inward to cover the anterior face of the squamosal wall. This flange, by accident or design, limits the posterior swing of the quadrate.

The specimen is looked upon as the property of the Geological Survey of Northern Rhodesia. However, according to an agreement it will eventually be decided which of the 496 specimens will be returned to Northern Rhodesia and which will, on account of their value to future research, be permitted to become integrated with the collection of the Bernard Price Institute. In the meantime all the specimens had been allocated field numbers which conform with the field catalogue of the Bernard Price Institute and the present specimen is numbered 3639 in our Karroo series. On account of its intrinsic value to both teaching and future research it is sincerely hoped that this specimen will be allowed to remain associated with its close relatives in the collection of the Bernard Price Institute.

Luangwa drysdalli gen. et sp. nov.

(Figure 15)

This new genus comes from a locality in the Ntawere Formation which is considerably higher than that of the previous specimen. While there may be doubts as to whether the previous specimen is actually above the *Cynognathus* zone, the present specimen is almost certainly of Molteno age. In fact, it has its closest ally in *Scalenodon* of the nearby Manda Beds of Tanganyika and it is

this relationship which influenced the conclusion that the bulk of the Ntawere Formation is of Manda or Molteno age. It is numbered 3727 in the Karroo Field Catalogue of the Bernard Price Institute and, as in the case of the previous specimen, it is hoped that, because of its scientific and teaching value, it will be permitted to remain in this collection. 3731

The specimen is fairly complete, but slightly crushed. Some surface damage, combined with problems encountered with preparation, where the matrix is rather coarse and in places difficult to distinguish from the bone as far as both colour and texture are concerned, makes finer structural interpretation somewhat problematic. Especially the palatal and basicranial regions are very difficult to interpret and the latter region is in addition obscured by some fragmentary and unidentifiable skeletal bones. In other places structural detail is merely ambiguous; certain features can be interpreted in more than one way. This should be borne in mind when referring to the accompanying figure. Proportions and shape are, however, quite reliably portrayed.

Damage, both artificial and natural, amounts to the following:

(*a*) Slight crushing affects the symphysial region.

(*b*) The nasal and premaxillary region has collapsed.

(*c*) Areas in the vicinity are cracked and it is difficult to follow sutures accurately.

(*d*) On the right side the extreme postero-lateral angle of the skull, including the articular region, is missing and indications are that it had very recently weathered away.

(*e*) Overall distortion is minimal.

The following is a comprehensive list of useful measurements (in mm.), some of which are based on reconstruction:

Total length of skull to squamosal flanges	150
From premaxillaries to posterior border of secondary palate	61
From premaxillaries to pterygoid processes	91
Distance from premaxillaries to posterior borders of orbits	95
Distance from premaxillaries to anterior borders of orbits	61
Distance from premaxillaries to pineal foramen	105
Distance from premaxillaries to interparietal notch	129
Breadth of snout	40
Interorbital width	34
Maximum breadth across orbits	89
Width across temporal arches	85
Width across parietals	17
Distance across pterygoid processes inclusive	40
From anterior tip of dentary direct to articular process	117
From anterior tip of dentary direct to angular process	91
From anterior tip of dentary direct to coronoid process	124

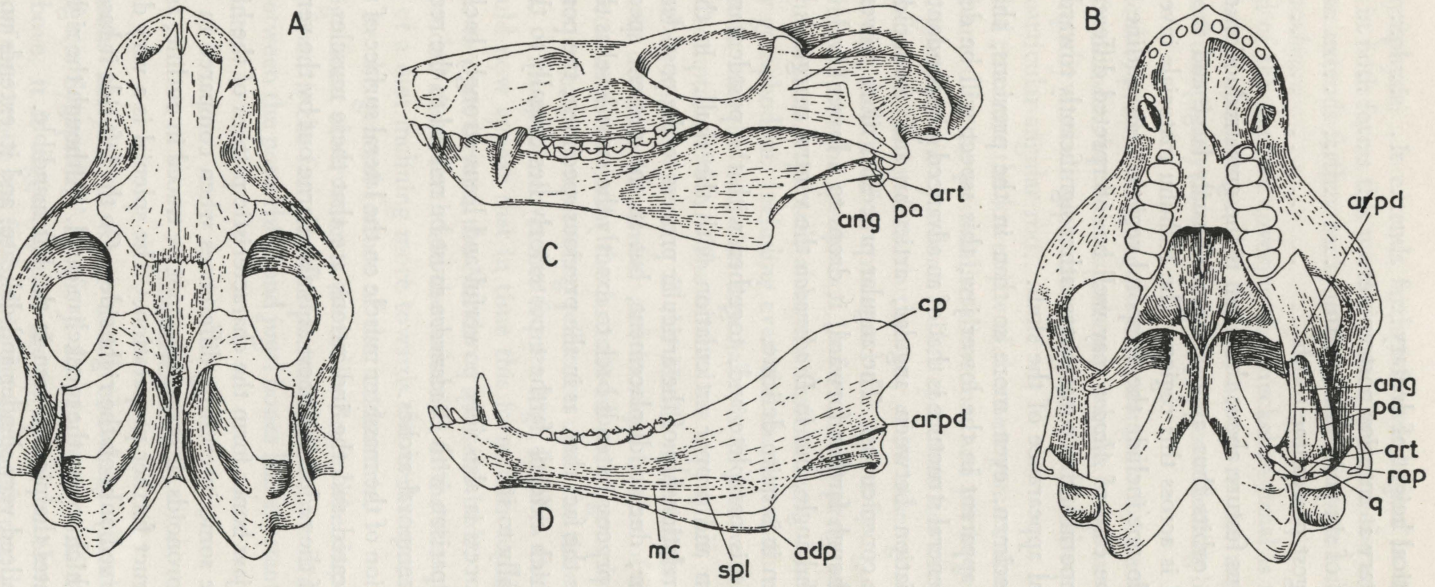


Fig. 15—The skull of *Luangwa drysdalli* gen. et sp. nov., ½ natural size. A, Dorsal view; B, Ventral view; C, Side view; D, Internal view of mandible. For abbreviations see figure 13.

Maximum vertical height of dentary	59
Height of dentary at anterior postcanines	15
Length of row of six postcanine teeth	35
Breadth of largest postcanine tooth	12

A very conspicuous feature about this skull is the great reduction of the temporal region. The orbits thus appear extraordinarily large and the maximum breadth of the skull is across this region. The Ruhuhu materials investigated by Crompton (1955) do not include the temporal region. His outline restoration of this region in the case of *Aleodon* may well be interpreted differently. This reduction of the temporal arches contributes rather significantly towards the more mammal-like general appearance of the skull.

Since in this specimen, even more so than in the previous, the advanced nature is especially apparent in the lower jaw, this aspect will be dealt with in more detail. The general structure is that of an advanced gomphodont cynodont, with the differentiation between angular, articular and coronoid processes equally if not more conspicuous. The angular process is more powerful than in *Diademodon* and, although farther forward, it drops to a lower level. It projects with a more powerful angle, but in *Diademodon* the ventral margin is heavier. In the present specimen it is quite delicate.

The left mandible is complete and, together with the postdentary bones, it is in good occlusion and proper articulation with the skull. In the previous specimen the exact relationship of the articular process to the post-dentary bones is somewhat unclear, due to displacement, but in the present specimen it is quite clear that this process extends back to exactly the same level as the articular itself. Interesting is the fact that, as in the previous specimen, the portion of the articular process which extends farthest posteriorly lies dorsally to the articular bone, and not laterally to it.

The coronoid process is also very powerful and leans strongly backward. Its lesser height in comparison with *Diademodon* must be related to the reduction and lower level of the temporal arches.

The area of insertion of the masseter muscle on the lateral surface of the dentary is very well demarcated and the indications are that these muscles were quite powerful, in spite of the reduced arches, as is also borne out by the very powerful cheek teeth.

The other lower jaw bones form the characteristic pattern of the higher cynodonts, but there are some interesting differences when compared in detail with *Diademodon*. The coronoids, if present, cannot be traced in outline, as the pterygoid processes obstruct further preparation. The splenial is a very delicate film of bone and is preserved only on the right side. On the left side it has fallen away to expose the fold which covers the meckelian canal. Although the right mandible is figured, it illustrates the picture seen in the left mandible.

The splenial is indeed very slender and delicate, and it extends up to but not

into the symphysis. It extends farther forward than in *Cricodon* (Crompton, 1955) but in both forms this portion would appear to be equally delicate. The splenial also extends farther back, in the shape of a more slender prolongation, than in *Cricodon*.

The fold of the dentary covering the meckelian canal is more extensive posteriorly than in *Diademodon*. It extends across to the angular process of the mandible and completely covers the small process reflecting back from the angular bone.

The articular, prearticular, angular and surangular form a structure very similar to that of *Diademodon*, but by comparison it is quite conspicuously smaller. There is not an equally distinct separation between the dorsal surangular rod and the ventral prearticular-angular rod.

In detailed structure the lower jaw of this new genus reflects a condition which is more advanced in the mammalian direction, and yet in general composition it is typically gomphodont cynodont. This specimen lies closer and farther along the line leading to the Ictidosauria than any of its other gomphodont allies.

As far as the skull itself is concerned the figures bring out as much detail as can be gathered from the specimen. Unfortunately preservation is unsatisfactory in some crucial areas, especially along the basicranium. The structure as a whole is typically gomphodont, including even the characteristic maxillary depressions on the snout, and the dentition especially is in line with that of the Ruhuhu material (Crompton, 1955). The canines are very small, while the cheek teeth are reduced in number to six. If the Manda material should indicate a trend towards both decrease in number and increase in size of the cheek teeth, the present specimen is no doubt the farthest advanced gomphodont on record and this observation casts an interesting reflection upon the time span of the Ntawere Formation. This specimen comes from a high level in the Ntawere Formation and it would now appear that in time this formation could extend from upper *Cynognathus* to even beyond the Manda or Molteno beds.

The expanded cheek teeth and the reduction in the size of the canines are also suggestive of a diet inclining more towards the herbivorous, aligning with what appears to be the general feature of the Ictidosauria.

A less significant observation is the rather *Bauria*-like shape of the postorbitals. More significant is the fact that the postorbital bars are fairly delicate, with the junction between the postorbital and jugal bones less substantial than in the lower gomphodonts.

Classification

For reasons analysed in more detail elsewhere (Brink: "The taxonomic position of the Synapsida," *S. Afr. J. Sci.*, in press) and supported by various remarks above, it is suggested that the Synapsida be elevated to Class status. The origin of this group lies far back in the Carboniferous, level with the earliest

amphibians and ancestral reptiles. In fact, Diapsid and Synapsid divergence occurred very early and ever since these two trends have remained well separated.

The promotion of the Synapsida is propagated here largely to overcome the difficulty of accommodating forms as widely different as *Ictidosuchus* and *Bauria*, or *Silphedestes* and *Luangwa*, in the same Infra-orders. It is becoming increasingly difficult, as more and more aberrant forms come to light, to classify these divergent directions with the assistance of the Super-family as the only rank available.

Tentatively, therefore, the following classification is suggested. Lower ranks can be introduced when required, as our knowledge of new forms expands.

Class Synapsida
- Subclass Pelycosauria
  - Order Ophiacodontia
  - Order Sphenacodontia
  - Order Edaphosauria
- Subclass Therapsida
  - Order Theriodontia
    - Suborder Titanosuchia
    - Suborder Gorgonopsia
    - Suborder Therocephalia
    - Suborder Scaloposauria
      - Infraorder Ictidosuchoidea
      - Infraorder Bauriamorpha
    - Suborder Cynodontia
      - Infraorder Procynosuchia
      - Infraorder Cynognathia
        - Superfamily Cynognathoidea
        - Superfamily Gomphodontoidea
    - Suborder Ictidosauria
  - Order Anomodontia
    - Suborder Deinocephalia
    - Suborder Venyukoviamorpha
    - Suborder Dromasauria
    - Suborder Dicynodontia

Besides elevating all groups by one rank, the two suborders Scaloposauria and Cynodontia are subdivided; otherwise in outline the above classification conforms with that suggested by Watson and Romer (1956), on which there are significant differences of opinion.

Watson (1957) also emphasises the pronounced gulf between the reptiles and mammal-like reptiles, which can be traced back to the level of the emergance of the first reptiles from the amphibians, in his subdivisions Sauropsida (including birds) and Theropsida (including mammals). The Sauropsida comprises the

earlier class Reptilia, with the class Aves as a later warm—blooded offshoot which had acquired class status in itself. The Sauropsida is, therefore, a superclass, combining two substantial classes. Similarly, and in terms of the proposal that the Synapsida should be promoted, the Theropsida is also a superclass combining an earlier largely cold-blooded stock, the class Synapsida, and its later warm-blooded offshoot, the class Mammalia.

Watson's (op. cit.) diagrammatic analysis also makes it substantially clear that both the "Bauriamorpha" and Cynodontia comprise two groups each. He designates the earlier group in the bauriamorph branch as the Scaloposauria, but the later group is not allocated a distinctive name at the same level. Similarly the earlier group in the cynodont branch is designated as the Procynosuchia, leaving the later group also without a distinctive name at the same classificatory level.

Both the "Bauriamorphs" and the cynodonts have thus far been accepted as infraorders, leaving only the rank of superfamily to accommodate what Watson (op. cit). should then have referred to as the Scaloposauroidea and Procynosuchoidea. Each of these two groups require room for accommodating several superfamilies in themselves and they can hardly rank at a lower level than infraorder.

In the classification suggested above Watson's Scaloposauria is translated into the infraorder Ictidosuchoidea (which includes *Scaloposaurus*) and this, together with the second infraorder Bauriamorpha, is placed in the suborder Scaloposauria. The Procynosuchia is looked upon as another infraorder, separate from the later infraorder Cynognathia, both forming the suborder branch Cynodontia. This arrangement in itself dictates a promotion of the Synapsida to class status.

Olson (1962) also seems to have difficulty in accommodating certain groups at various taxonomic levels. These difficulties seem to arise from his inclination to demote rather than promote certain groups, and is the result of the introduction of additional ranks at the more senior levels. Olson's taxonomic suggestions will certainly become more simplified and a great deal more acceptable if he would be prepared to accept the Synapsida as a substantial class.

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